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Growth Rate and Maturation of Skeletal Muscles over a Size Range of Galliform Birds

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ABSTRACT

The relationship between growth rate and development of function in leg and pectoral muscles was studied in four species of galliform birds ranging from 125 g to 18 kg and, for comparison, in an altricial species, the European starling (80 g). An index to neonatal maturity (muscle dry content proportion as a fraction of adult value) was higher in leg than in pectoral muscles and lower in larger than in smaller galliforms. The maturity index was substantially lower in starling neonates. After the first week posthatch, however, the maturity index was highest in larger species. Exponential growth rates decreased linearly with increasing maturity in both pectoral and leg muscles, following similar regressions in all species including the starling. At a particular value of the maturity index, the exponential growth rate was higher in pectoral than in leg muscles. The exponential growth rates of muscles of neonatal large galliforms were lower than expected from their low maturity. This may represent the down-regulation shortly after hatching of the high exponential growth rate needed to reach a large hatching mass in a short incubation period. A slower growth rate immediately posthatch may be necessary if the relatively immature neonatal digestive system cannot deliver nutrients or metabolized energy required for more rapid growth. Smaller species may not be faced with the constraint of rapid growth toward the end of the embryonic period.

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Introduction

Growing organisms must allocate tissue, nutrients, and energy between growth and mature function (Ricklefs 1979, 1983). There is an inverse correlation between the growth rate of muscle and indices of muscle function during postnatal growth (Ricklefs et al. 1994). Species having different levels of functional maturity at hatching (i.e., precocial and altricial) nonetheless exhibit similar relationships between growth rate and mature function, although the neonates of these species occupy different points on the line relating growth rate and function. This consistency suggests that a generalized growth rate/functional maturity relationship may constrain the evolutionary diversification of postnatal development.

Among birds, large species take longer to develop than small species (Ricklefs 1968). Longer development periods result in part from the fact that the chicks of large species hatch at a smaller percentage of adult mass (Rahn et al. 1975) and therefore have farther to grow. However, large species also have lower relative, or percentage, growth rates at any particular relative size (i.e., size relative to adult mass). Thus, rate constants of equations fitted to growth data are lower for large species than for small species (Ricklefs 1972, 1979; Starck and Ricklefs 1997*a*). If a single growth rate/functional maturity constraint applies to all birds regardless of their adult body size, then one would expect the chicks of large species to achieve a particular level of functional maturity at a smaller size relative to the adult than the chicks of small species.

In this study, we examine the relationship between growth rate and development of function in the leg and pectoral muscles of four species of galliform birds, ranging in adult mass from the Japanese quail, *Coturnix coturnix japonica* (about 125 g), northern bobwhite, *Colinus virginianus* (150 g), and guinea fowl, *Numida meleagris* (2.8 kg), to the domesticated turkey, *Meleagris gallopavo* (18 kg). These species therefore represent more than a 100-fold range in adult body mass from the smallest to the largest. European starlings, *Sturnus vulgaris* (80 g), were included in the analysis to provide a comparison with a species having altricial development. Growth rates of muscles were determined from dissections of a series of chicks of each species. The functional capacity of a muscle at a particular age was estimated by its dry matter content (Ricklefs et al. 1994), which has been found to correlate with changes in enzyme activities, force production, and metabolic heat production (Choi and Bakken 1991; Choi et al. 1993). In this study, we first ask whether the relationship

between growth rate and dry matter content of muscles is similar in species of different sizes and different developmental patterns. We then compare the increase in dry matter content during the postnatal growth period between large and small species. We use these comparisons to test the hypothesis that the lower growth rate constants of larger precocial species are related to the maturation of skeletal muscle at a lower proportion of adult size.

Material and Methods

Animals and Housing

Fresh eggs of turkey (B.U.T. Big 6 strain) and guinea fowl (Galor strain) were obtained from commercial breeders and incubated at the Department of Veterinary Basic Sciences, University of Utrecht. Hatchlings were left up to 8–12 h posthatch in the incubator (37.5°C), after which they were maintained in accordance with standard breeding conditions (Dietz 1995). Water and commercial food were supplied ad lib.

Neonates of Japanese quail and bobwhite were purchased from a commercial farm and maintained in animal facilities at the University of Pennsylvania with water and quail starter food supplied ad lib. Nestling European starlings were obtained from nest boxes maintained at the Morris Arboretum farm, Montgomery County, southeastern Pennsylvania. Nestlings were brought into the laboratory at 9:00–11:00 A.M., kept at 32°–35°C, and fed to maintain body mass until they were subjected to metabolism measurements (Choi et al. 1993) and then killed.

Sampling

In turkey and guinea fowl, six chicks were killed at each of the following ages: turkey, 0, 3, 6, 11, 20, 27, 70, and 240 ($N = 12$) d; guinea fowl, 0, 3, 6, 10, 15, 20, 27, 50, and 167 ($N = 11$) d. In bobwhite, Japanese quail, and starling, one to five chicks were killed at each of the following ages (values are given as day:sample size; the values in parentheses were pooled and the ages averaged): bobwhite, (0:2, 1:3), 4:4, 7:4, 10:4, (13:2, 14:4), (20:2, 21:4), and 38:4 d; Japanese quail, (0:3, 1:2), 4:5, (6:1, 7:3), 10:4, (14:3, 15:3), (19:2, 20:3), 25:2, and 37:4 d; starling, 0:3, 3:3, 6:4, 9:3, (12:3, 13:1), 15:3, and 20:2 d. The oldest birds of each species are referred to as the "ultimate" sample. Except in the bobwhite, these birds had achieved nearly adult mass, and the size and functional capacity of their muscles were also assumed to be similar to those of adults.

Dissection and Handling of Tissues

Immediately after each chick was killed, we excised from one side of the body the pectoral muscles and as much as possible of the leg muscles between the junction of the femur with the body and the distal end of the tibia. The muscles were weighed to the nearest 0.001 g. In addition, in large individuals of the turkey and the guinea fowl, the gastrocnemius and iliotibialis muscles (from the lower leg and upper leg or thigh, respectively) were removed, weighed, and retained for further analysis.

Muscle masses of turkeys and guinea fowl were freeze-dried to constant mass. In the other species, muscle masses were dried to constant mass at 60°–65°C. Lipids were extracted from the dried muscles by petroleum ether extraction (40°–60°C) in the case of the turkey and guinea fowl, and by petroleum ether : chloroform (5 : 1) extraction in the other species. Fresh and dry masses were converted to lipid-free values. Including chloroform in the extraction solvent removes a maximum of an additional 5% from the dry weight of the muscle tissues compared with petroleum ether alone (R. E. Ricklefs, unpublished data). Over the range of lipid-free dry fractions reported in this study, differences in extraction solvents would result in differences in lipid-free dry fraction of 0.005–0.001, which is generally less than the variation in values within age-groups and much less than differences between age-groups. The dry fractions of the gastrocnemius and iliotibialis muscle did not differ significantly within any age and species category. We therefore assumed that their dry fractions were representative of all leg muscles.

Chicks of turkey and guinea fowl were sexed. Although adult turkeys are highly sexually dimorphic, neither the masses nor dry fractions of either muscle in either species differed significantly (t-test, unequal variances, $P > 0.05$) between males and females through 70 d in the turkey and through 167 d in the guinea fowl. Accordingly, data for males and females were pooled. Masses of male and female turkeys were averaged to obtain ultimate values; dry fractions did not differ significantly between the sexes. Quail and starlings do not exhibit marked sexual size dimorphism as adults, and chicks were not sexed.

Growth Analysis

For analysis of growth, all masses (g) were converted to natural logarithms. For each species, averages of the logarithms of mass were calculated for each age. Total logarithmic growth increments between the neonatal and ultimate samples were calculated as the difference between the natural logarithms of the masses at each point. The logarithmic growth increment is the natural logarithm of the ratio of the final to the initial value, and therefore it is the natural logarithm of the factor by which a component has grown over an interval. Dividing the logarithmic growth increment by the length of the interval gives the average exponential rate of growth during the interval. The variance of the growth increment was estimated as the sum of the variances of ultimate mass and neonatal mass, and the standard error as the square root of the summed variances divided by the square root of the summed sample sizes. For each age interval (age i to age f), average exponential growth

rates were calculated as the logarithmic growth increment $[\ln(W_f) - \ln(W_i)]$, where W is body mass, divided by the length of the interval between samples. A reference mass for each growth interval was calculated as the average of the mass at the beginning and end of the interval. A reference dry fraction for each interval was calculated in the same manner. Because our data are analyzed over intervals, the total sample size is equal to the sum of the intervals for all the species ($N = 34$).

Growth rate constants (k) were estimated by fitting the differential form of the Gompertz growth equation, $d\ln(W)/dt = -k\ln(W/A)$, to interval data, where W is the mass at any given age, $d\ln(W)/dt$ is the exponential growth rate of the muscle during any given age interval, and A is the asymptotic value. Coefficients of this equation were estimated by linear regression analysis of the relationship between exponential growth rate and reference mass among the age intervals (see Ricklefs 1983, 1985). Sample sizes were the number of age intervals (6 or 7).

Ultimate values for masses of the entire body and each of the muscles and their dry fractions were the mean values for individuals at ages 244 d (turkeys, $N = 12$), 167 d (guinea fowl, $N = 11$), 39 d (bobwhite, $N = 4$), 38 d (Japanese quail, $N = 4$), and 21 d (starling, $N = 2$). An index of maturity was calculated for each muscle tissue at each age as the proportion of the ultimate value.

Statistical Analyses

Two individual sample means were compared by t-test. Groups of sample means were compared by ANOVA or by ANCOVA where size was a covariate. The dependence of exponential growth rate of each of the muscle masses on the maturity index and species was determined by ANCOVA. All analyses were carried out with procedures of the Statistical Analysis System Institute (SAS Institute 1988).

Results

Comparison of Adults and Neonates

Measurements of neonates and birds in the ultimate samples are presented for each of the five species in Table 1. Logarithmic growth increments were positively correlated with ultimate body mass ($F = 148$, df = 1, 7, $P < 0.001$; Fig. 1), and they were larger for pectoral muscles than for leg muscles ($F = 136$, df = 1, 7, $P < 0.001$). In galliforms, the growth increments of the leg muscles were similar to those of the body as a whole ($F = 4.5$, df = 1, 5, $P = 0.09$). In the starling, the growth increment of the leg muscles (2.79) substantially exceeded that of the body as a whole (1.29; $t = 16.8$, df = 8, $P < 0.001$). Growth increments of the starling body mass and pectoral muscles were smaller than those of the two species of quail ($t > 15$, df = 12, $P < 0.001$ for all four comparisons); growth increment of the leg muscles of the starling (2.79) was more nearly similar to that of the bobwhite (2.68; $t = 1.2$, df = 12, $P > 0.2$) and also the Japanese quail (2.95, $t = 4.7$, df = 12, $P < 0.001$). The proportions that the pectoral muscles make up of the entire body mass of galliform neonates did not appear to differ between large and small species (turkey, 1.3%; guinea fowl, 0.6%; bobwhite, 1.5%; Japanese quail, 1.2%). However, the leg muscles were a larger proportion of the body in the quail (bobwhite, 8.2%; Japanese quail, 7.5%) than in the larger species (turkey, 5.7%; guinea fowl, 4.5%). Proportions of the muscles of the starling neonate (pectoral, 1.2%; leg, 3.5%) were similar to those of the larger galliform neonates. Leg muscles of the neonates of all the species were 1.0–1.5 natural log units (i.e., 2.7–4.5 times) larger than the pectoral muscles ($t > 6$, df = 8 or 10, $P < 0.001$).

Among the neonates of the galliform species, dry fractions of the pectoral muscles were lower in the two larger species than in the two quail ($t > 7.6$, df = 9, $P < 0.001$). In addition, the dry fraction of the leg muscles of turkey neonates was lower than those of the neonates of the other three species, but not significantly so ($t = 0.6$–1.0, df = 9, $P > 0.2$). As we expected, the dry fractions of the muscles of neonates of the altricial starling were lower than those of neonates of the precocial galliform species; however, none of the differences was statistically significant (leg: $t = 0.8$–1.5, df = 6 or 9, $P < 0.02$; pectoral: $t = 0.0$–1.3, df = 6 or 7, $P > 0.2$). The dry fractions of the ultimate samples did not differ markedly among the species; values for the pectoral muscles tended to be higher than those for the leg muscles (pectoral − leg = 0.026 ± 0.0065 SD, $N = 5$, $t = 8.9$, $P < 0.001$).

Gompertz Growth Constants

The growth rates of the pectoral muscle masses did not differ significantly between the species of galliforms ($k = 0.058$ d^{-1} in the turkey to 0.083 d^{-1} in the bobwhite; Table 1). Growth rates of the pectoral muscles of the starling were higher ($k = 0.080$ d^{-1}), but not significantly so, than those of the larger galliforms ($t = 1.4$, 1.7; df = 14, 13; $P > 0.1$). In another study (Ricklefs et al. 1994), growth rate constants were estimated by nonlinear curve-fitting of Gompertz equations to the relationship of the logarithm of muscle mass to age. Values of the growth rate constant calculated by this method for the pectoral muscles of bobwhite, Japanese quail, and starling were 0.068, 0.072, and 0.122 d^{-1}, respectively. Values for the two quail match those obtained in this study even though the confidence limits for the latter were very broad (coefficients of variation of the mean = 0.41 and 0.89). In conclusion, this study found little evidence for variation among the species in the growth rate constants of pectoral muscle masses, even considering the comparison between the altricial starling and the precocial galliforms.

Table 1: Attributes of the muscle masses of neonates and ultimate samples

	Japanese Quail[a]	Bobwhite[a]	Guinea Fowl	Turkey	Starling
Neonate (age, sample size)	.4, 5	.6, 5	0, 6	0, 6	0, 3
Ultimate (age, sample size)	37, 4	38, 4	167, 11	244, 12	20, 2
Body:					
Ln neonate mass (SD)	1.95 (.14)	1.84 (.09)	3.48 (.06)	4.06 (.07)	2.30 (.13)
Ln ultimate mass (SD)	4.84 (.03)	4.57 (.07)	7.94 (.09)	9.80 (.34)	4.22 (.04)
Ln increment (SEM)	2.89 (.04)	2.73 (.02)	4.46 (.02)	5.64 (.07)	1.92 (.05)
Pectoral muscle:					
Ln neonate mass (SD)	−2.25 (.25)	−2.76 (.21)	−1.60 (.20)	−.27 (.11)	−2.11 (.45)
Ln ultimate mass (SD)	3.32 (.05)	2.98 (.06)	5.29 (.11)	7.53 (.39)	2.57 (.11)
Ln increment (SEM)	5.57 (.06)	5.74 (.04)	6.89 (.04)	7.79 (.08)	4.68 (.06)
Neonate dry fraction (SD)	.141 (.016)	.139 (.023)	.118 (.031)	.104 (.009)	.105 (.039)
Ultimate dry fraction (SD)	.241 (.003)	.262 (.005)	.268 (.006)	.257 (.027)	.279 (.004)
Maturity index of neonate	.585	.530	.440	.405	.376
Gompertz growth constant (k) (SEM)	.066 (.059)	.083 (.034)	.061 (.010)	.058 (.007)	.080 (.017)
Leg muscles:					
Ln neonate mass (SD)	−.64 (.21)	−.66 (.19)	.37 (.09)	1.20 (.14)	−1.06 (.42)
Ln ultimate mass (SD)	2.95 (.02)	2.68 (.11)	5.28 (.15)	7.15 (.35)	1.73 (.00)
Ln increment (SEM)	2.95 (.02)	2.68 (.11)	4.91 (.03)	5.95 (.07)	2.79 (.05)
Neonate dry fraction (SD)	.175 (.038)	.188 (.041)	.174 (.015)	.158 (.016)	.138 (.035)
Ultimate dry fraction (SD)	.206 (.006)	.232 (.001)	.241 (.016)	.237 (.008)	.259 (.012)
Maturity index of neonate	.850	.801	.722	.667	.533
Gompertz growth constant (k) (SEM)	NA	.058 (.036)	.041 (.005)	.029 (.002)	.159 (.018)

Note. Age is in days, and body mass is in grams.

[a] The samples of neonates included two 0-d and three 1-d chicks in the case of the bobwhite, and three 0-d and two 1-d chicks in the case of the Japanese quail.

The growth rate of the leg muscles varied significantly among the species. The lowest value of the growth rate constant among the galliforms, that for the turkey (0.029 d^{-1}), was significantly less than that for the guinea fowl (0.041 d^{-1}; $t = 3.1$, df = 15, $P < 0.01$). The standard error of the growth rate constant of the bobwhite (0.058 ± 0.036 d^{-1}) was too large to reveal statistically significant differences compared with the other galliforms. In the Japanese quail, the relation between exponential growth rate and reference mass over age intervals, which is used to estimate the growth rate constant, was not significant. Therefore, a Gompertz growth rate parameter could not be estimated. According to the technique of Ricklefs et al. (1994), this value was 0.052, which is similar to that of the bobwhite. In the starling, the values were 0.159 ± 0.018 in this study and 0.172 in the analysis of Ricklefs et al. (1994). Thus, the leg muscles of the starling grow several times more rapidly than do those of the galliforms included in this study ($t > 3.5$, df > 12, $P < 0.01$).

Muscle Maturity

Maturity of muscle tissue in the neonate (i.e., dry proportion relative to adult dry proportion; Fig. 2) was lower in the pectoral muscle than in the leg muscle (ANCOVA, $F = 185$, df = 1.5, $P < 0.0001$), and it was lower in the larger species than in the smaller species ($F = 46$, df = 1.5, $P < 0.0001$). As one would expect, the muscles of the starling, particularly the leg muscle, had even lower maturity indices (leg: $t > 4.1$, $P < 0.01$). The maturity index increased rapidly with age in all species, exceeding 0.8 between 1 and 11 d in the case of the leg muscles and between 10 and 15 d in the case of the pectoral muscle (Fig. 3*a, d*). The maturity indices of the leg and pectoral muscles were higher with respect to growth remaining ($\ln[W/A]$) in the turkey and, to a lesser extent, in the guinea fowl than in the two smaller quail because the neonates of larger species are a smaller proportion of final (ultimate) mass (Fig. 3*c, f*). Maturity indices of starling muscles were substantially lower than those of the galliforms relative to the fraction of growth remaining, as would be expected of a species with altricial development. The starling differed from the galliforms in that muscle maturity did not approach its ultimate level until growth had been nearly completed.

Exponential Growth Rate and Muscle Maturity

The relationship between exponential growth rate and maturity index was analyzed in an ANCOVA in which species was the

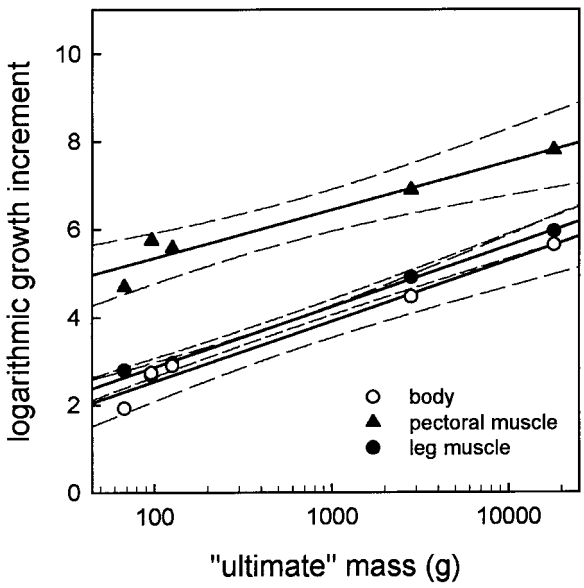

Figure 1. Allometric relationship between the overall logarithmic growth increment and ultimate (adult) body mass (U) for the pectoral and leg muscles and the body as a whole. Equations are as follows: log(body mass) = −0.22 (±0.39 SEM) + 1.38 (±0.13 SEM) log(U); log(pectoral muscles mass) = 3.16 (±0.50 SEM) + 1.09 (±0.17 SEM) log(U); log(leg muscles mass) = 0.09 (±0.19 SEM) + 1.38 (±0.06 SEM) log(U).

main effect and maturity was the covariate (Fig. 4). The total sample consisted of 34 growth intervals in the five species. In neither the pectoral nor the leg muscles was the interaction between species and maturity index a significant effect (Table 2). In subsequent ANCOVAs without interactions, species was not a significant effect for either pectoral muscles or leg muscles; maturity index was a significant effect in both cases. When the analyses were rerun as simple linear regressions of exponential growth rate as a function of maturity index, the relationships were significant, but relatively weak, for both the pectoral muscles (r^2 = 0.25) and leg muscles (r^2 = 0.19).

Although exponential growth rate and maturity index were significantly negatively related, the data exhibited considerable scatter. Much of this scatter results from a lag in muscle growth immediately after hatching, when growth rate is typically low in precocial species (see, e.g., Ricklefs and Weremiuk 1977). Another part of the scatter could be attributed to the 7–8-d sample of Japanese quail, in which muscle masses were very large. This caused the preceding growth increment to be unexpectedly high and the following growth increment to be low. These birds came from a different hatch than the others and may have been incorrectly aged. Therefore, the regressions of exponential growth rate on maturity index were calculated again without the Japanese quail, with a lower bound for maturity index of 0.6, which eliminated the first one or two growth increments of each species, and with an upper bound for exponential growth rate of 0.6. This left a sample of 22 growth intervals in four species. In spite of the smaller samples and narrower range of values, however, the new regression statistics were more highly significant for both the pectoral muscles (Table 2; r^2 = 0.70) and the leg muscles (r^2 = 0.63). Again, neither species effects nor species × maturity interactions were significant.

The regressions had the following form: exponential growth rate = $a + b$(maturity index). The intercepts of the regressions (a) were 0.90 (±0.11 SEM) and 0.61 (±0.08 SEM) for the pectoral and leg muscles, respectively. The slopes of the regressions (b) were −0.85 (±0.12 SEM) and −0.56 (±0.09 SEM), respectively. The slope of the regression for the pectoral muscles significantly exceeded that for the leg muscles. The slopes of the regressions were approximately equal to the intercepts, and the value of exponential growth rate consequently decreased to 0 when the maturity index was approximately 1. Therefore, for any given level of maturity, exponential growth rates of pectoral muscles were higher than those of the leg muscles.

Discussion

The results of this study are consistent with a generally inverse relationship between exponential growth rate and functional maturity of skeletal muscles (Ricklefs and Webb 1985; Ricklefs et al. 1994), although the relationship differed between leg

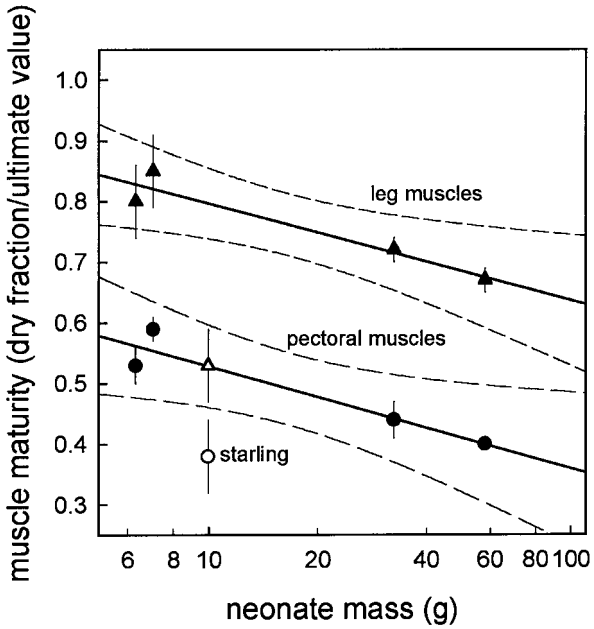

Figure 2. Relationship between neonatal maturity index (M) and neonatal body mass for the pectoral (*circles*) and leg muscles (*triangles*). *Open symbols*, starling. Equations are as follows: M(leg muscles) = 0.96 (±0.05 SEM) − 0.16 (±0.04 SEM) log(neonate mass); and M(pectoral muscles) = 0.70 (±0.05 SEM) − 0.17 (±0.04 SEM) log(neonate mass); starling was excluded for each regression.

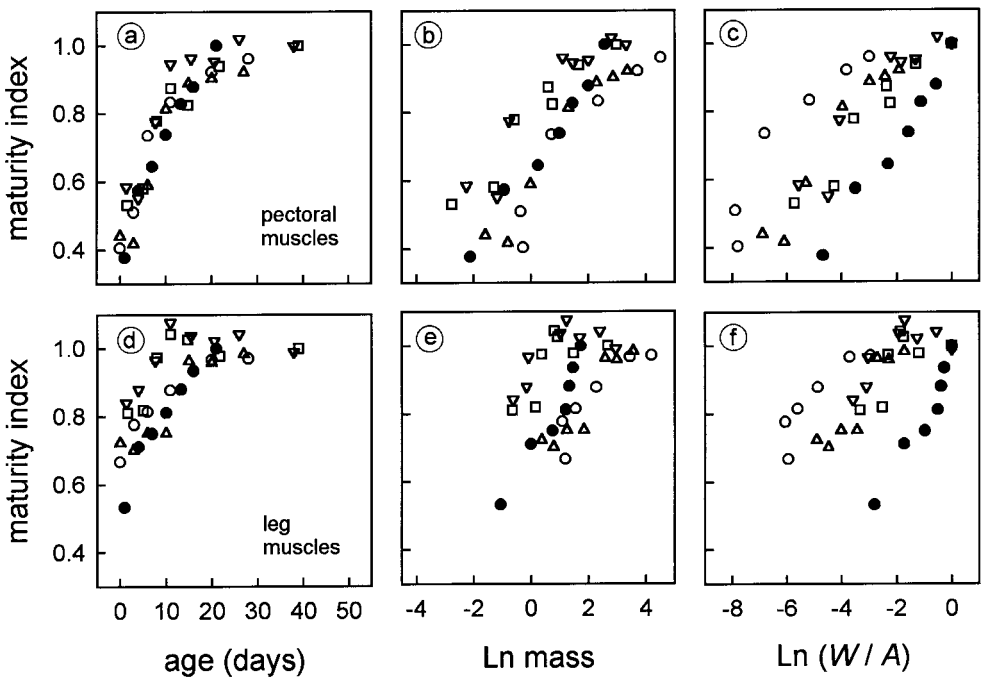

Figure 3. Increase in the maturity index of the pectoral and leg muscles with respect to age (*a, d*), the natural logarithm of muscle mass (*b, e*), and the natural logarithm of the muscle mass relative to its adult size (*W/A; c, f*). Species are turkey (*open circles*), guinea fowl (*right-side-up triangles*), bobwhite (*squares*), Japanese quail (*upside-down triangles*), and starling (*solid circles*).

and pectoral muscles. For a given maturity index, which is proportional to the relative dry matter content of the tissue, the pectoral muscles exhibited growth that occurred about 1.5 times faster. This difference may result from differences in the structure of the two kinds of muscles, for example, different proportions of connective tissues, densities of blood vessels, or densities of mitochondria in the muscle fibers (Pennycuick and Rezende 1984; Armstrong and Laughlin 1985; Rosser and George 1986). Such factors may affect the growth rate of muscle tissue. Alternatively, the growth rates of one or both muscle masses may be differently regulated below the physiologically maximum rate during the postnatal growth period.

Because large species hatch at a relatively small proportion of adult mass, the increments of postnatal growth are large compared with those of smaller species. In addition, the maturity indices of the neonates are lower in the two larger galliforms than they are in the smaller quail (Fig. 5). According to the hypothesis of a growth rate/functional maturity constraint, low neonatal maturity should permit more rapid growth of tissues shortly after hatching. Contrary to this expectation, however, neither the turkey nor the guinea fowl showed such a response. In both species, the growth rates of both leg and pectoral muscles were less than the expected exponential growth rate extrapolated from the relationship of exponential growth rate to maturity index among older individuals during the first week posthatch (Fig. 4). Thus, the low maturity index at hatching of the larger species is not associated with an increase in the growth rate of the muscles at this time. Possibly, growth is slowed during the period of transition from embryonic to postembryonic life, or growth rate of the skeletal muscles is regulated downward during this period because some other part of the body limits overall growth rate at this time. After the first week posthatch, the growth rate and maturity index are closely related in each of the muscle masses, and this relationship appears to be similar for the species considered in this study, including the altricial European starling (Fig. 4).

One possible explanation for the slow growth of the large galliform species, in spite of the low maturity indices of their tissues, is that the perinatal period is one of rapid change in tissue function that accompanies the transition from embryonic to postnatal life. This period of rapid perinatal change may be incompatible with rapid tissue growth. This idea is supported by the rapid increase of the maturity index shortly after hatching in the larger species. Within a week, the maturity indices in the turkey were higher at a given fraction of adult mass achieved than they were in the two quail species and in the guinea fowl (Fig. 3*c, f*). This is consistent with the lower Gompertz growth rate constant for the leg muscles in the turkey (0.029) compared with those of the guinea fowl (0.041) and, especially, the bobwhite (0.058). The low maturity indices of the muscles of the altricial starling throughout the growth period are consistent with the higher exponential growth rates and Gompertz growth rate constant observed in that species.

A second possible explanation for the slow growth of turkeys

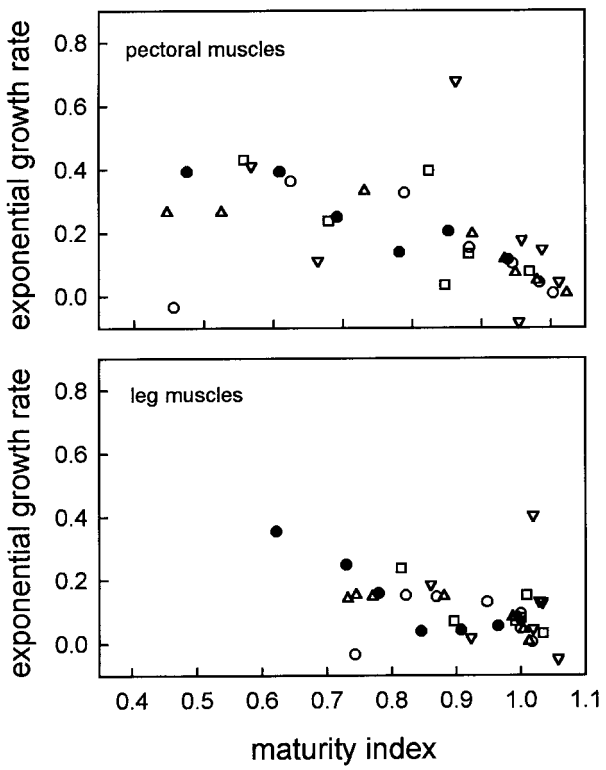

Figure 4. Relationship between exponential growth rate and maturity index for pectoral muscles (*top*) and leg muscles (*bottom*). Species are turkey (*open circles*), guinea fowl (*right-side-up triangles*), bobwhite (*squares*), Japanese quail (*upside-down triangles*), and starling (*solid circles*).

and guinea fowl immediately posthatch is that, like the skeletal muscles, the digestive system is not fully functioning during this transition period, and it cannot supply enough metabolizable energy to support both increased activity and respiratory metabolism of the young chick and a high growth rate. Although neonates can rely on the resources of the yolk sac, as many do during the first day posthatch, food intake is important. Without adequate assimilation of ingested food, chicks may starve or suffer undernutrition. Furthermore, food intake may enhance thermoregulation, as suggested by the results of Decuypere and Kühn (1988). Delayed functional maturation of tissues during embryonic development will affect not only the muscles of the neonate but also other tissues, such as those of the digestive system (Starck and Ricklefs 1997*b*). Consequently, the assimilation rate of the neonate may be low, at a time when increasing function of the digestive system is important for further development. Several studies on domestic fowl (Murakami et al. 1992; Obst and Diamond 1992; Nir et al. 1993) and domestic turkeys (Kroghdahl and Sell 1989) show that digestion, food intake, and growth are low immediately after hatching but increase rapidly during the early part of the postnatal development period. This increase in functional maturity of the digestive system may very well limit the growth potential of the chick as a whole.

The decrease in neonatal maturity index with increasing adult and neonate size observed in this study is consistent with the results of a broader survey of the dry fractions of neonate tissues (Starck and Ricklefs 1997*b*). This same relationship occurs in other groups of precocial and semiprecocial birds, including shorebirds (Scolopacidae), seabirds (Procellariiformes), and ducks (Anatidae). The reasons for this trend are unclear. On one hand, large size may allow the evolution of a less capable neonate. That is, neonates of larger species may be under less stringent selection for functional capacity than those of smaller species because their large size makes temperature regulation easier and perhaps makes the chicks less vulnerable to predators. On the other hand, the results of this study show that the relationship between size and maturity is reversed soon after hatching by rapid increase in the maturity index in larger species. Thus, two different phenomena must be explained: why large species hatch at a low maturity index, and why large species have higher maturity indices throughout most of their postnatal growth period.

Low neonatal maturity index may be linked to rapid embryonic development. Predation and other sources of mortality favor a shorter incubation period that is, compared with the postnatal growth period, potentially a more dangerous time. According to the hypothesis of a growth rate/functional matu-

Table 2: Results of ANCOVAs of the relationship between exponential growth rate and maturity index

	Pectoral Muscle			Leg Muscle		
	df	*F*	*P*	df	*F*	*P*
Species × maturity index interaction	4, 24	.50	.73	4, 24	1.30	.30
Species effect without interaction	4, 28	.05	.74	4, 28	.80	.54
Regression of exponential growth rate on maturity index without species effect	1, 32	10.6	.0027	1, 32	7.30	.011
Regression of exponential growth rate on maturity index in selected data set	1, 20	47.5	.0001	1, 24	41.4	.0001

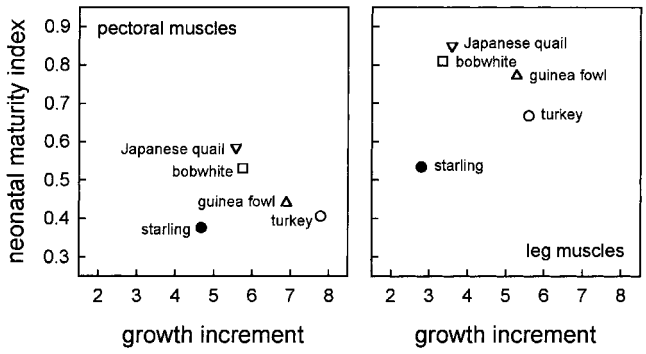

Figure 5. Relationship between neonatal maturity index and logarithmic growth increment for pectoral muscles (*left*) and leg muscles (*right*).

rity trade-off, one way that embryonic growth rate could be increased during the latter part of the incubation period would be to forestall the functional maturation of muscles and other tissues until after the chick has hatched. Independent of adult mass, neonate mass is about 67% of egg mass (Ar and Rahn 1985). Within taxonomic orders, the length of the incubation period increases only as the 0.11 power of egg mass or neonate mass (Ricklefs 1993). Because embryo mass increases as about the cube of incubation time in most species of birds (Ricklefs 1987; Ricklefs and Starck 1997), the relationship between incubation period and size is expected to have a power of 0.33, about three times that actually observed, if larger and smaller neonates merely represented different points on the same growth process. Thus, interspecific comparisons of neonate mass and incubation period suggest that embryos of larger species reach their neonatal mass with higher exponential growth rates than do smaller species, even though it takes them slightly longer because their neonatal masses are larger. At first glance, this may seem a paradox. Higher embryonic exponential growth rates may be brought about through delaying the functional maturation of tissues.

The high maturity indices of large species during most of postnatal growth are consistent with their longer postnatal development periods and lower growth rate constants, compared with smaller species. In part, longer development periods result from the larger postnatal growth increments of larger species. For example, the logarithmic growth increment of the leg muscles of the turkey was almost twice (or 100-fold in absolute terms) that of the two species of quail. Even if the turkey and quail had similar Gompertz growth rate constants, the postnatal development period of the turkey would considerably exceed that of the quail: the turkey simply has more growing to do. In addition to the larger growth increment, however, the turkey and, to a lesser extent, the guinea fowl also exhibit higher maturity indices throughout most of the growth period. According to the growth rate/functional maturity hypothesis, this should result in a lower exponential growth rate at any particular point on the growth curve. Consistent with this idea, the Gompertz growth rate constants of the leg muscles were lower for the larger species.

Why should larger species grow more slowly? Slower growth may reduce daily energy and nutrient requirements, allowing chicks to subsist on lower quality diets and providing greater safety margins in case of decrease in food supply. Presumably slower growth is less dangerous for larger species, which already at hatching are large enough to escape many potential predators of chicks and resist or tolerate extreme climates. For smaller species, high mortality rates favor adaptations, such as reduced functional maturity, that allow the chick to pass more quickly through the vulnerable development period.

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Literature Cited

Ar A. and H. Rahn. 1985. Pores in avian eggshells: gas conductance, gas exchange and embryonic growth rate. Respir. Physiol. 61:1–20.

Armstrong R.B. and M.H. Laughlin. 1985. Muscle function during locomotion in mammals. Pp. 56–63 in R. Gilles, ed. Circulation, Respiration and Metabolism. Springer, Berlin.

Choi I.-H. and G.S. Bakken. 1991. Locomotion and muscle function during postnatal development of the northern bobwhite (*Colinus virginianus*): effect of body temperature. Physiol. Zool. 64:653–672.

Choi I., R.E. Ricklefs, and R.E. Shea. 1993. Skeletal muscle growth, enzyme activities, and the development of thermogenesis: a comparison between altricial and precocial birds. Physiol. Zool. 66:455–473.

Decuypere E. and E.R. Kühn. 1988. Alterations in thyroid hormone physiology induced by temperature and feeding in newly hatched chickens. Acta Physiol. Pol. 39:380–394.

Dietz M.W. 1995. Development of metabolism and thermoregulation in galliforms: effects of body mass, growth rate and functional maturity. PhD thesis, University of Utrecht, The Netherlands.

Kroghdahl Å. and J.L. Sell. 1989. Influence of age on lipase, amylase, and protease activities in pancreatic tissue and intestinal contents of young turkeys. Poult. Sci. 68:1561–1568.

Murakami H., Y. Akiba, and M. Horiguchi. 1992. Growth and utilization of nutrients in newly-hatched chick with or without removal of residual yolk. Growth Dev. Aging 56:75–84.

Nir I., Z. Nitsan, and M. Mahagna. 1993. Comparative growth

and development of the digestive organs and of some enzymes in broiler and egg type chicks after hatching. Br. Poult. Sci. 34:523–532.

Obst B. and J. Diamond. 1992. Ontogenesis of intestinal nutrient transport in domestic chickens (*Gallus gallus*) and its relation to growth. Auk 109:451–464.

Pennycuick C.J. and M.A. Rezende. 1984. The specific power output of aerobic muscle, related to the power density of mitochondria. J. Exp. Biol. 108:377–392.

Rahn H., C.V. Paganelli, and A. Ar. 1975. Relation of avian egg weight to body weight. Auk 92:750–765.

Ricklefs R.E. 1968. Patterns of growth in birds. Ibis 110:419–451.

———. 1972. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115:177–201.

———. 1979. Adaptation, constraint and compromise in avian postnatal development. Biol. Rev. 54:269–290.

———. 1983. Avian postnatal development. Pp. 1–83 in D.S. Farner, J.R. King, and K.C. Parker, eds. Avian Biology. Vol. 7. Academic Press, New York.

———. 1985. Modification of growth and development of muscles from a comparative viewpoint. Poult. Sci. 64:1563–1576.

———. 1987. Comparative analysis of avian embryonic growth. J. Exp. Zool. Suppl. 1:309–323.

———. 1993. Sibling competition, hatching asynchrony, incubation period, and lifespan in altricial birds. Curr. Ornithol. 11:199–276.

Ricklefs R.E., R.E. Shea, and I.-H. Choi. 1994. Inverse relationship between functional maturity and exponential growth rate of avian skeletal muscle: a constraint on evolutionary response. Evolution 48:1080–1088.

Ricklefs R.E. and J.M. Starck. 1997. Embryonic development. Pp. 31–58 in J.M. Starck and R.E. Ricklefs, eds. Avian Growth and Development: Evolution within the Altricial-Precocial Spectrum. Oxford University Press, New York.

Ricklefs R.E. and T. Webb. 1985. Water content, thermogenesis, and growth rate of skeletal muscles in the European starling. Auk 102:369–376.

Ricklefs R.E. and S. Weremiuk. 1977. Dynamics of muscle growth in the starling and Japanese quail: a preliminary study. Comp. Biochem. Physiol. 56A:419–423.

Rosser B.W.C. and J.C. George. 1986. The avian pectoralis: histochemical characterization and distribution of muscle fiber types. Can. J. Zool. 64:1174–1185.

SAS Institute. 1988. SAS/STAT user's guide, release 6.03 ed. SAS Institute, Cary, N.C.

Starck J.M. and R.E. Ricklefs. 1997*a*. A data set of avian growth parameters. Pp. 379–421 in J.M. Starck and R.E. Ricklefs, eds. Avian Growth and Development: Evolution within the Altricial-Precocial Spectrum. Oxford University Press, New York.

———. 1997*b*. Patterns of development: the altricial-precocial spectrum. Pp. 3–30 in J.M. Starck and R.E. Ricklefs, eds. Avian Growth and Development: Evolution within the Altricial-Precocial Spectrum. Oxford University Press, New York.